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Modulation of the N170 adaptation profile by higher level factors

Stefan Schinkel[a,b,*], Galina Ivanova[c], Jürgen Kurths[b,d,e], Werner Sommer[a]

[a] *Department of Psychology, Humboldt-Universität zu Berlin, Germany*
[b] *Department of Physics, Humboldt-Universität zu Berlin, Germany*
[c] *Department of Computer Science, Humboldt-Universität zu Berlin, Germany*
[d] *Potsdam Institute for Climate Impact Research (PIK), Germany*
[e] *Institute for Complex Systems and Mathematical Biology, University of Aberdeen, United Kingdom*

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ABSTRACT

Event-related potentials provide strong evidence for a face-specific process that peaks at about 170 ms following stimulus onset – the N170 effect. The N170 has been shown to be sensitive to adaptation, reflected in an amplitude reduction by repeated face presentation, which is usually considered to be driven by bottom-up processes. Here we investigated whether the N170 adaptation profile can be modulated by top-down factors aiming at holistic or feature-based processing. Adaptor stimuli were Mooney faces, isolated facial features (eyes or mouths), or houses. Target faces required either a gender decision (holistic task), or a decision on a facial feature (detail task). We observed an intricate crossover interaction pattern, reflected in opposite effects on adaptation to Mooney faces and eyes as compared to mouth conditions. These findings provide evidence that adaptation effects can be modulated by top-down processes.

1. Introduction

Faces play a vital role for human beings. Extraction of features such as a person's identity, motivation, or intentions is a key requirement for humans as a social species and allows them to adapt to their environment. Being able to process faces in dedicated neural systems is therefore likely to provide an evolutionary advantage. Functional brain imaging has indeed uncovered such a dedicated network, located on the inferotemporal lobe, more precisely in the fusiform gyrus (FG). It is commonly referred to as the fusiform face area (FFA). The FFA has repeatedly been reported to show stronger activation to faces than to non-face objects (e.g. Kanwisher, McDermott, & Chun, 1997). In event-related brain potentials (ERPs) the processing of facial stimuli is reflected in the face-selective N170 component, a negative deflection peaking around 150–200 ms after stimulus onset over temporo-occipital sites (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Since its discovery the N170 has been studied intensely, mostly because it seems to be uniquely sensitive to faces. The N170, as well as the M170, the magnetoencephalographic (MEG) equivalent, are commonly related to structural face encoding (Bentin & Deouell, 2000; Bentin et al., 1996; Eimer, Gosling, Nicholas, & Kiss, 2010). Due to its sensitivity to faces, the N170 can be considered as reflecting early, face-selective cortical processes (Eimer, 2011). The N170 shows right-hemisphere lateralization and has been reported to be sensitive to manipulations of face inversion (Bentin et al., 1996; Eimer, 2000; Itier & Taylor, 2002) and facial ethnicity (Caldara, Rossion, Bovet, & Hauert, 2004).

Neural adaptation is a powerful method to study the response properties of neurons and larger neuronal populations (Grill-Spector, 2006; Henson, Shallice, & Dolan, 2000). It is observed when identical or categorically equivalent items are presented in rapid succession and is reflected in a modulation, usually a reduction of the strength, of the neural response to the following item. While the underlying mechanisms are not yet fully understood (Grill-Spector, 2006; Grillspector, Henson, & Martin, 2006) the paradigm has successfully been used in ERP studies on the processing of faces, where adaptation is reflected in a decreased amplitude of the N170 (Kovács et al., 2006). More recently Eimer (2011) could demonstrate that in comparison to non-faces stimuli (houses), upright and inverted schematic faces and black and white Mooney faces adapted the N170 to naturalistic gray-scale faces. Furthermore they could show that N170 adaptation effects reflect the activation of face-selective neurons by full faces as well as by individual face parts, such as the eyes.

In an MEG study, the M170 showed adaptation to full faces, scrambled faces, and isolated face parts as adaptors (Harris & Nakayama, 2008). Notably, these authors did not find adaptation effects to line drawings of face configurations. Harris & Nakayama's

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* Corresponding author at: Department of Psychology, Humboldt-Universität zu Berlin, Germany. Tel.: +49 30209399121.
E-mail address: schinkel@physik.hu-berlin.de (S. Schinkel).

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data suggest that M170 adaptation reflects adaptation to featural, but not congurational face information whereas Eimer's data suggest that N170 adaptation reflects both.

In a recent study, Nemrodov and Itier (2011) employed a rapid adaptation paradigm to investigate the face inversion effect on the N170. In this paper they tested predictions from the neural model of face processing by Itier and colleagues (Itier, Alain, Sedore, & McIntosh, 2007; Itier & Batty, 2009) and the orientation-sensitivity hypothesis (OSH, Eimer, Kiss, & Nicholas, 2010). The OSH suggests, that the N170 might also reflect the activity of neurons that are sensitive to deviations from canonical stimulus orientations. In this study Nemrodov and Itier (2011) used various upright and inverted face types as adaptor stimuli and inverted faces as test stimuli. They showed that different modulations of the test stimuli were found only when eyes were present in the adaptors. Their study stresses the importance of the eyes, which they suggest to act as anchor points from which the generation of the face percept starts.

In a study on face orientation and familiarity, with and without task relevance of identity, Anaki, Zion-Golumbic, and Bentin (2007) investigated the impact of attentional or strategical manipulation on the N170. They concluded that the N170 marks the initial detection of faces and might trigger further processes but stress that these processes cannot be modulated by attentional or strategical manipulations. This is in accordance with previous studies that suggest that the processes giving rise to the N170 cannot be modulated by attention or other high level manipulations (Carmel & Bentin, 2002; Cauquil, Edmonds, & Taylor, 2000). Nonetheless, this is not undisputed and an indication for a possible penetration was found in repetition priming of familiar and unfamiliar faces (Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003).

The lack of reported top-down effects on the N170 supports the idea of an automatic mechanism. The findings of strong adaptation effects do not contradict this notion because adaptation is considered to relate to low-level and bottom-up mechanisms such as neuronal fatigue. Interestingly there seem to be no studies on top-down influences on adaptation effects. If the N170 adaptation effects were entirely automatic one would not expect top-down effects, for example by different tasks that require different strategies of processing such as holistic or part-based processing requirements. If such an effect did occur it would argue for a cognitive, top-down modulation of these seemingly low-level effects.

2. Experiment

Here we aimed to assess whether the N170 adaptation profile can be modulated by top-down cognitive factors. More specifically, we tested whether the N170 adaptation profile is affected when requiring either holistic or feature-specific processing of facial stimuli.

We used four different adaptor stimuli – presentation of a house, a Mooney face, isolated eyes, and isolated mouth. Sample adaptors are shown in Fig. 1a. While Mooney face adaptors do have features, those have to be processed holistically, as opposed to single features. In contrast, isolated mouths aimed at adapting this particular feature without holistic component and houses were assumed to have no face-related adaptation effect. Eye adaptors may have a special status because despite being isolated features they may trigger holistic processes because they may represent relational information, e.g. of size and distance, and hence may trigger holistic processes (Maurer, Grand, & Mondloch, 2002). Two different experiments, a gender and a detail decision experiment, were carried out. In the gender decision task, participants had to indicate whether the test stimuli showed a male or a female face and in the detail decision task participants were asked to distinguish whether or not teeth were visible in the target face stimuli. Sample test stimuli are shown in Fig. 1b. We assumed that the gender decision triggers holistic processing whereas the decision about the mouth triggers feature-based, top-down processing. If the different processing strategies enforced by the task – presented block wise – exert a top-down modulation of the specific adaptation processes induced by the adaptors, one would expect an enhancement of holistic adaptation by Mooney faces in the (holistic) gender decision. On the other hand mouth-induced adaption should be enhanced in the detail decision. For eye-induced adaptation we expected more pronounced effects in gender than in detail decisions. This is based on the assumption that pairs of eyes are processed as configurations rather than details (Itier et al., 2007). Participants performed the gender decision task first because in analyses to be reported elsewhere we aim to relate the present findings to individual differences in brain anatomy.

2.1. Methods

2.1.1. Participants

Nineteen adults (5 female), aged 20–28 (mean 24.2 ± 2.3 years) participated in an ERP study. All were right-handed (according to Oldfield, 1971) with normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. They signed an informed consent according to the institutional review board of Humboldt-Universität and received either course credit or were paid for participation.

2.1.2. Stimuli and presentation

The adaptor stimuli were gray scale images depicting either houses, Mooney faces, isolated eyes, or mouths (Fig. 1). The isolated features eyes/mouths were presented in their canonical position. Mooney faces were constructed by converting gray scale images of natural faces to black and white images with a fixed threshold (40%). Test stimuli were gray scale pictures of male and female faces with a neutral expression. For the detail task a slightly opened mouth showing teeth was morphed into half the faces. All stimuli were presented within an elliptical mask and matched for luminance. The angular size of the images was $4.4^\circ \times 6.6^\circ$.

Participants sat at a viewing distance of about 1 m from the computer screen on which stimuli were presented using Presentation software (NeuroBehavioral Systems). A fixation cross was shown for 500 ms indicating the beginning of a trial. Then an adaptor was shown for 200 ms followed by a blank screen for 200 ms and the stimulus for 200 ms. The intervals are identical to the ones used by Eimer, Gosling, et al. (2010). After the presentation of the target participants had 1000 ms to classify the stimulus according to gender or the visibility of teeth, using buttons. The buttons were randomly assigned to male/female or the visible/not visible alternatives at the beginning of the experiment and changed halfway through the experiment. The gender decision and the detail decision task were performed in two successive runs. For the adaptors there were 4 levels with 6 items that where presented with 12 distinct targets, of which half depicted females, in all possible combinations. This yields a total of $6 \times 4 \times 12 = 288$ trials. In the detail decision, again all adaptors (6×4) where shown with 12 target faces of which 6 showed teeth. Half of the faces showing teeth were females as was the case for the faces not showing teeth. Again all possible combinations for adaptors and targets were shown, yielding a total of 288 trials as well. Consequently for every adaptor in every task $n = 72$ trials were recorded.

2.1.3. EEG acquisition and analysis

The EEG was recorded from 126 Ag/Ag–Cl electrodes (impedance $\leq 5\,\mathrm{k}\Omega$) at a sampling rate of 1000 Hz using a BrainAmp DC amplifier (Brain Products GmbH, Munich, Germany) with a time constant of 10 s and high cut-off at 250 Hz. All electrodes

(a) Sample adaptor stimuli (b) Sample test stimuli

Fig. 1. (a) Sample adaptors used in the experiment. Adaptors were chosen such that they either did not trigger face processing at all (house), trigger holistic processing (Mooney) or detail processing (mouth). Whether eyes presented in isolation trigger holistic or detail processing has not been fully clarified yet. (b) Sample test stimuli used in the experiment. The details, open mouth versus closed mouth, were morphed into the faces. Subjects had to judge whether the person depicted was male or female (holistic task) or whether or not teeth were visible (feature-specific task).

Table 1
Mean peak N170 amplitudes in μV and latency in ms to adaptor stimuli split by task and item. Standard deviation in parentheses.

	Amplitude			Latency		
	Gender	Detail	Mean	Gender	Detail	Mean
House	−3.60 (3.30)	−2.08 (3.97)	−2.84 (3.68)	165.84 (15.07)	165.37 (21.76)	165.61 (18.46)
Mooney	−10.85 (4.68)	−11.13 (3.99)	−10.99 (4.29)	156.16 (11.97)	160.74 (11.38)	158.45 (11.75)
Mouth	−6.99 (3.21)	−6.57 (3.92)	−6.78 (3.54)	165.89 (14.30)	172.68 (16.22)	169.29 (15.47)
Eyes	−9.39 (4.17)	−8.35 (4.17)	−8.87 (4.14)	159.47 (14.12)	164.21 (12.38)	161.84 (13.32)
mean	−7.70 (4.70)	−7.03 (5.14)		161.84 (14.27)	165.75 (16.24)	

were initially referenced to an electrode on the left mastoid (A1). Off-line the data was converted to average reference, by subtracting the mean of all channels. For the analysis the EEG data was band-pass filtered from 0.1 to 30 Hz. Trials with artifacts or incorrect responses were excluded. N170 amplitudes were quantified relative to the mean activity in a 100 ms time window from 50 ms before the presentation of the stimulus to 50 ms for targets (following Eimer, Gosling, et al., 2010) and relative to a 100 ms window preceding the presentation of the stimulus for adaptors. The N170 amplitudes were automatically detected as local minima between 150 and 250 ms post-stimulus at the electrodes P08 and P07 (center of highlighted electrodes in Fig. 3). The N170 peak latency was the time point of the detected N170 peak. Analogously, the P1 component was detected as a local maximum between 50 and 150 ms post-stimulus. For the analysis of hemispheric effects we included two electrodes next to P08/P07, as shown in Fig. 3. We chose these electrodes sites as they are known to best reflect the N170 effect. We chose to *a priori* define the electrodes used for statistical testing as it is (1) firmly grounded in theory and previous results and (2) avoids decomposition of omnibus tests and the correction for multiple testings associated with such an approach.

2.1.4. Statistical analysis

The N170 peak latencies and peak amplitudes as well as reaction times were analyzed using linear mixed effect modeling (LME, Bates & Watts, 1988) in *R* (R Core Team, 2013). We fitted models with task and adaptor as fixed effects and a random effect for subjects. For the analysis of hemispheric differences, the LME was extended by a further fixed effect for hemisphere. The significance of main effects and interactions was then assessed by *F*-tests. We chose to use LMEs instead of repeated measures ANOVAs as LMEs are better at handling random effects (subjects) than repeated measures ANOVAs, and do not require a sphericity correction. *Post hoc* analysis were permutation tests (Good, 2005) for equal means implemented in MATLAB (The Mathworks, 2010, Natwick MA) or *t*-tests with Tukey correction for multiple comparisons.

2.2. Results

2.2.1. Behavioral results

The overall error rate was negligible (≤3%) across adaptors and tasks. In terms of mean reaction times we found a main effect of task (gender = 494 ms, detail = 448 ms, $F_{(1,126)} = 51.98$, $p < 0.0001$). The main effect of adaptor was not significant ($F_{(3,125)} = 1.46$, $p > 0.05$), as was the interaction task×adaptor ($F_{(3,125)} = 0.06$, $p > 0.05$) (Fig. 2).

2.2.2. N170 to adaptors

The main effect of task on the N170 amplitude to adaptors was significant ($F_{(1,126)} = 4.14$, $p = 0.04$) indicating larger amplitudes in the gender than in the detail task as was the main effect of adaptor ($F_{(3,126)} = 110.36$, $p < 0.0001$). A *post hoc*, pairwise comparison of the N170 peak amplitudes (Table 2) revealed that, in line with theory, the house adaptor did not elicit a noticeable N170, which in fact was smaller than that to all other stimuli. The Mooney faces elicited a larger N170 than isolated mouths. The N170 elicited by pairs of eyes was intermediate between Mooney faces and mouths and did not significantly differ from either adaptor.

We further investigated the N170 peak latency in adaptor-elicited ERPs, where latencies in the detail task were larger than in the gender task ($F_{(1,126)} = 7.20$, $p = 0.0082$). We could further observe a significant effect of adaptor ($F_{(3,126)} = 10.36$, $p < 0.0001$) but no interaction ($F_{(3,126)} = 1.12$, $p > 0.05$). *Post hoc* testing revealed that the main effect of adaptor in this case was due to significantly longer

Table 2
Post hoc comparisons of N170 peak amplitude to adaptors (across tasks). Comparisons were conducted using a permutation test for equal means with Bonferroni adjusted alpha levels (0.05/6 =0.0083).

Combination	*p*	*z*	
House × eyes	0.000	Inf	***
House × mouth	0.000	Inf	***
House × mooney	0.000	Inf	***
Mooney × mouth	0.000	-Inf	***
Mooney × eyes	0.026	−2.226	n.s.
Mouth × eyes	0.020	2.326	n.s.

*** Highly significant.

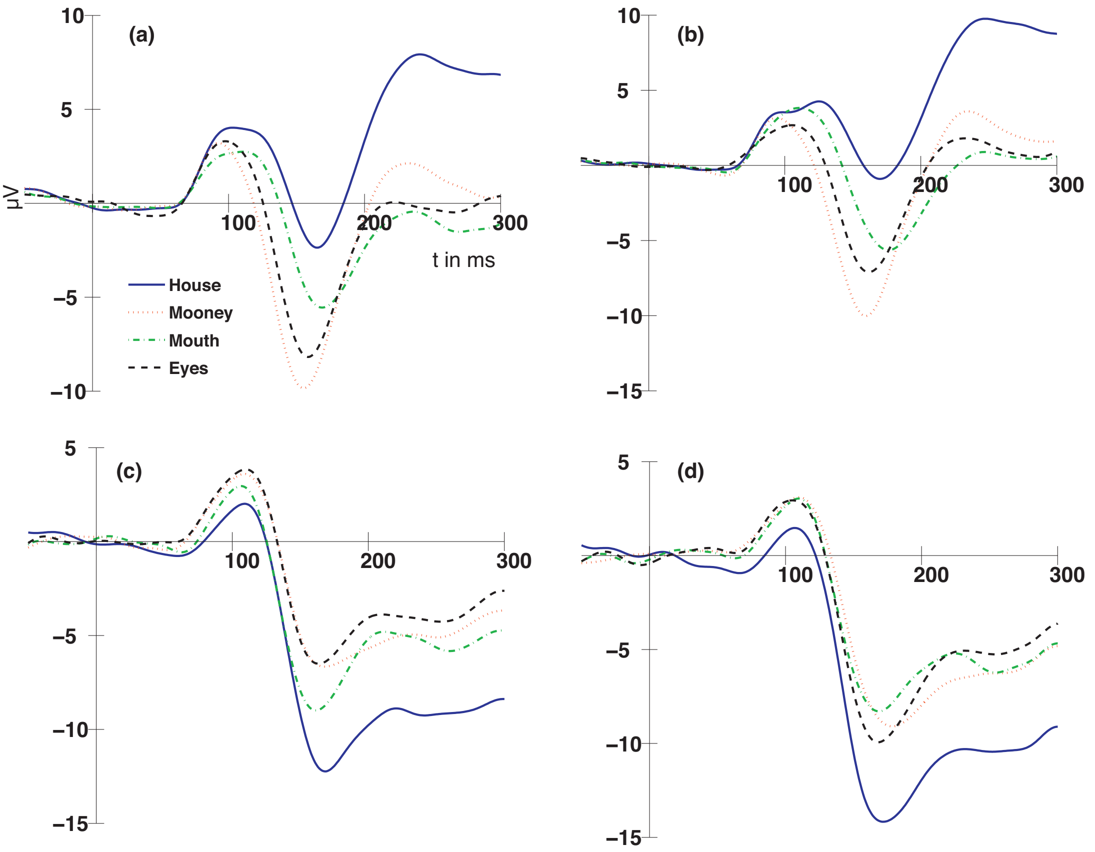


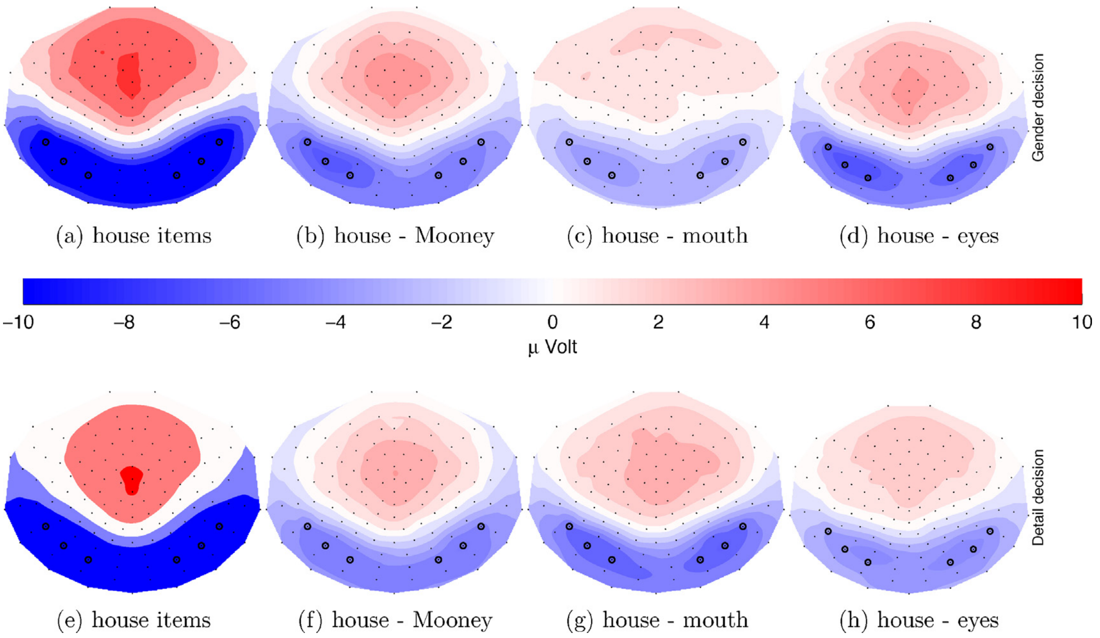
Fig. 2. Grand average ERPs at electrode site PO8 to adaptor stimuli (top panels) and test stimuli (bottom panels) as a function of adaptor condition.

latencies of mouth adaptors in comparison to Mooney adaptors and also in comparison to eye adaptors (Table 1).

Summarizing the effects on the N170 to adaptors, we found larger N170 amplitudes and longer latencies in the detail task and importantly, there were no interaction effects.

2.2.3. *P1 to test stimuli*

For the P1 amplitude the main effect of task was reflected in a significantly larger amplitude in the gender than in the detail task ($F_{(1,126)} = 22.52$, $p < 0.0001$) and also observed a main effect of adaptor ($F_{(3,126)} = 15.73$, $p < 0.0001$). *Post hoc* testing revealed a



(a) house items (b) house - Mooney (c) house - mouth (d) house - eyes

(e) house items (f) house - Mooney (g) house - mouth (h) house - eyes

Fig. 3. Topographies of the N170 to faces following a neutral adaptor (a, e) and of the N170 adaptation effect (house minus item) in the gender (top) and detail decision task (bottom). The electrodes used for assessing the hemispheric differences are highlighted.

Table 3
Mean peak P1 amplitudes in μV to test stimuli split by task and item. Standard deviation in parentheses.

	Gender	Detail	Mean
House	3.38 (2.92)	2.19 (2.57)	2.78 (2.78)
Mooney	5.06 (2.70)	4.23 (2.43)	4.64 (2.57)
Mouth	3.66 (1.97)	3.17 (2.24)	3.42 (2.09)
Eyes	4.91 (2.56)	3.47 (1.96)	4.19 (2.36)
Mean	4.25 (2.62)	3.27 (2.38)	

significant difference between house and eye adaptors ($p = 0.01$), and between house and Mooney face adaptors ($p < 0.0001$) because after house adaptors the P1 was smaller than for the other adaptors apart from mouth adaptors which were in-between. Importantly, there was no interaction ($F_{(3,126)} = 0.99$, $p < 0.399$) with task (Table 3).

2.2.4. N170 to test stimuli

The main effects of adaptor and task on N170 amplitude to test stimuli were significant (task: $F_{(1,126)} = 28.27$, $p < 0.0001$, adaptor: ($F_{(3,126)} = 70.30$, $p < 0.0001$). Importantly, the interaction task × adaptor was significant as well ($F_{(3,126)} = 8.12$, $p = 0.001$). *Post hoc* testing revealed that the main effect of adaptor was primarily due to the neutral adaptor condition house, which had not elicited an N170 upon its presentation and hence left the N170 to target faces unattenuated. As a follow-up, we omitted the level house in the factor adaptor. The main effect of adaptor vanished ($F_{(2,90} = 0.38$, $p > 0.05$). However, the main effect of task was significant ($F_{(1,90)} = 19.52$, $p < 0.0001$) as was the interaction with adaptor ($F_{(2,90)} = 12.91$, $p < 0.0001$). As this interaction might be primarily due to the level mouth in the adaptor factor, we also omitted the mouth level, retaining only two levels of the factor adaptor (Mooney face and eye). Indeed, the interaction vanished ($F_{(1,54)} = 3.9$, $p > 0.05$).

To ensure that the findings are not due to the order of the tasks, we further fitted LMEs, testing for interactions in the comparison mouth vs. eyes, mouth vs. Mooney and eyes vs. Mooney. If such interactions appear it is unlikely that they are due to the global effect of fatigue or practice induced by the constant task order in the present manuscript. It turned out that we indeed found interactions for all comparisons that included the level mouth. The comparison mouth vs. eyes yielded a main effect of task ($F_{(1,54)} = 8.4$, $p = 0.005$) and a significant interaction ($F_{(1,54)} = 22.4$, $p < 0.0001$). For mouth vs. Mooney face adaptors only the interaction was significant ($F_{1,54} = 13.2$, $p = 0.0006$). In the case of eye adaptor vs. Mooney face adaptors no interaction was found (Table 4). A detailed *post hoc* comparison can be found in Appendix.

We also investigated the N170 peak latency to target stimuli. The main effects task was not significant ($F_{(1,126)} = 0.49$, $p > 0.05$) but the main effect of adaptor was ($F_{(3,126)} = 3.90$, $p = 0.01$). Furthermore we found a significant interaction task × adaptor $F_{(3,126)} = 3.26$, $p = 0.02$). *Post hoc* testing revealed 2 significantly different combinations of task × adaptor mouth (gender) vs. mooney (gender) ($z = -3.14$, $p < 0.05$) and mouth (gender) vs. Mooney (detail) ($z = -3.37$, $p < 0.05$).

In summary, the core findings on the N170 to test stimuli were a larger N170 in the detail than in the gender task, an adaptor effect only for non-house stimuli and, importantly, an interaction of task and adaptor. This interaction turned out to be a crossover interaction carried by the mouth adaptors in comparison with the Mooney face/eye adaptors. In terms of latencies, the N170 following mouth adaptors in the gender task peaked significantly earlier than the N170 following Mooney adaptor in either task.

2.2.5. N170 topographies

We further investigated topographies of the N170 adaptation effect using the average peak amplitude across ROIs on both sides of the head. The ROIs comprised three electrodes, next to and including PO7 and PO8 respectively. For a 4-level factor adaptor we again observed a main effect of task ($F_{(1,270)} = 187.44$, $p < 0.0001$), a main effect of adaptor ($F_{(1,270)} = 62.64$, $p < 0.0001$) and an interaction of task × adaptor ($F_{(3,270)} = 15.33$, $p < 0.0001$). We further found a main effect of hemisphere, with the right hemisphere showing a larger amplitude (right: −10.1 μV, left: −9.1 μV, $F_{(1,270)} = 22.48$, $p < 0.0001$). All other 2-way interactions and the 3-way interaction were not significant.

To assess the actual adaptation effect we investigated the amplitude difference of house minus adaptor which yielded a 3-level factor adaptor (house-Mooney, house-mouth, house-eyes). The factors task and hemisphere remained the same. The main effects of task vanished ($F_{(1,198)} = 0.01$, $p > 0.05$), as did the main effects of adaptor ($F_{(2,198)} = 2.55$, $p > 0.05$) and hemisphere ($F_{(1,198)} = 3.26$, $p > 0.05$). We still observed a significant interaction of task×adaptor ($F_{(2,198)} = 30.32$, $p < 0.0001$) and additionally found an interaction of task × hemisphere ($F_{(1,198)} = 6.58$, $p = 0.011$). The interaction of adaptor×hemisphere and the 3-way interaction task×adaptor×hemisphere were not significant.

To verify that the task × hemisphere interaction was indeed only present in the actual adaptation effect, we investigated the N170 amplitude only to test stimuli following neutral (house) adaptors, which yielded a 2-level factor task and a 2-level factor hemisphere. Indeed we only found a main effect of task ($F_{(1,54)} = 20.39$, $p < 0.0001$) with larger negativity in the detail task than in the gender task. The main effect of hemisphere was not significant ($F_{(1,54)} = 3.76$, $p > 0.05$) as was the interaction of task and hemisphere ($F_{(1,54)} = 0.3$, $p > 0.05$).

Summarizing the results on the N170 topographies, we found larger amplitudes in the right than in the left hemisphere and observed an interaction of task and hemisphere if and only if the adaptation effect was observed in the first place.

3. Discussion

We investigated whether the adaptation profile of the putatively face-specific ERP component, the N170, can be modulated by cognitive demands. Explicitly we investigated if the adaptation profile of the N170 depends on whether participants engaged in holistic (gender decision) or in feature specific (detail decision) processing of test stimuli.

Table 4
Mean peak N170 amplitudes in μV and latency in ms to test stimuli split by task and item. Standard deviation in parentheses.

	Amplitude			Latency		
	Gender	Detail	Mean	Gender	Detail	Mean
House	−13.78 (4.29)	−15.79 (3.94)	−14.78 (4.19)	171.05 (17.82)	176.11 (20.50)	173.58 (19.12)
Mooney	−8.80 (4.01)	−10.69 (3.62)	−9.74 (3.89)	184.74 (31.38)	186.00 (29.52)	185.37 (30.06)
Mouth	−10.41 (3.05)	−9.64 (3.66)	−10.02 (3.35)	167.05 (23.31)	180.05 (32.48)	173.55 (28.65)
Eyes	−8.09 (4.26)	−11.32 (3.42)	−9.70 (4.15)	183.32 (35.81)	171.89 (21.27)	177.61 (29.62)
Mean	−10.27 (4.44)	−11.86 (4.30)		176.54 (28.46)	178.51 (26.44)	

In accordance with the literature we did not find an N170 to house adaptors as opposed to Mooney faces and isolated facial features (eyes and mouths). This aligns with evidence that the N170 is indeed sensitive to faces or face parts in their canonical position. Interestingly, isolated eyes did not show a larger N170 than Mooney faces. This is at variance with findings that whole realistic faces elicit smaller N170 than isolated eyes (Bentin et al., 1996) and might be due, on the one hand, to the fact that we used Mooney faces, whose features have to be processed holistically rather than pictures of faces with features in a face-typical configuration. On the other hand, in the eye conditions we used only eyes as adaptors, whereas previous research cropped a horizontal bar from portraits including the eyes and eyebrows (e.g., Nemrodov & Itier, 2011).

The N170 to adaptors was sensitive to the task. Such a sensitivity was already reported by Jacques and Rossion (2007) where low attentional load was found to elicit larger (more negative) N170 amplitudes. In the present study we found that the N170 amplitude to adaptors was globally smaller in the gender decision task. This could indicate that the detail decision task induced higher attentional load. However, we cannot rule out that this global task effect without interaction with condition reflects the fixed condition order. Alternatively, it could be an effect of long term habituation since the first block contained a larger number of faces already. In our setup we can therefore only interpret the *interaction effect*. One speculative explanation for this interaction is an enhanced adaptor quality for task-relevant properties–stimulus properties relevant for a given task have a stronger adaptive power. In alignment with previous research we found increased N170 latencies when attention was directed to the lower half of the face (Letourneau & Mitchell, 2008) that is, in the detail decision task. However, it is also possible, that the smaller N170 in the detail decision task is due to a long-term order effect because this condition always followed the gender decision (cf. Korinth, Sommer, & Breznitz, 2013).

The P1 preceding the N170 to test stimuli was affected by the experimental manipulation only in terms of the task and the adaptor items. Recent evidence (Dering, Martin, Moro, Pegna, & Thierry, 2011) suggests, that the P1 my be related to facial processing. Our findings could either be due to this sensitivity of the P1 or the fact that it is only enhanced, when the following N170 is adapted. The current setup does not allow us to clearly disentangle this. A different possible explanation could be the larger positivity after house adaptors. It is conceivable that this induced a kind of ceiling effect for further positive-going components. Important for our research question, the P1 component did not show interaction effects.

The analysis of the N170 amplitudes for test stimuli revealed a main effect of adaptor, a main effect of task and an interaction of task × adaptor. This main effect of adaptor turned out to be entirely due to the neutral adaptor, the house item, which is obvious since the house adaptor does not induce an N170 and therefore no adaptation was observed. This is again a confirmation, even though an indirect one, of the face sensitivity of the N170 ERP component.

In terms of our main question, whether a top-down manipulation (task) of bottom-up processes (neural adaptation) is possible, the core observation is the interaction between task and adaptor. This interaction is present for all comparisons that involve the mouth adaptor, which turned out to be the driving factor for the interactions. The task had opposite effects on adaptation to Mooney faces and eyes as compared to mouth conditions. Specifically, N170 amplitude to test faces following adaptation to mouths was larger in the gender than detail task, but was larger in the detail than gender task following adaptation to Mooney faces and eyes. We can therefore conclude, that there is indeed an influence of task on the N170 amplitudes for test stimuli and hence that neural adaptation effects can indeed be modulated by processing strategies required by the task. Tentatively we interpret this finding to indicate that attention to a certain stimulus property enhanced the adaptation effect of that property. Thus in the detail task, the adaptation effect due to the mouth was enhanced relative to the gender task. Conversely, in the gender task, requiring holistic processing, the adaptation effect of the Mooney faces was enhanced relative to the mouth task.

Note that the interaction between task and adaptor cannot be accounted for by general effects due to the order of the task. The core question surrounding these findings is why the N170 adaptation profile can be modulated higher level factors. While the impact of higher level factors on the N170 is currently under dispute, with some authors claiming automaticity of the process (Cauquil et al., 2000; Jemel et al., 2003), there are no studies that investigated the N170 adaptation profile under such manipulations. On the other hand, there is mounting evidence about top-down effects on early processes, for example task effects on processing of emotional facial expressions (Rellecke, Sommer, & Schacht, 2013) or knowledge effects on early visual ERPs (e.g. Rabovsky, Sommer, & Abdel Rahman, 2012).

It could be argued that the detail task directs the attention to the lower part of the face, reducing the influence of the eyes and hence diminishing the N170 amplitude. If this was the case, the N170 amplitude to eye adaptors should be reduced, but increased to mouth adaptors in the detail task. As we did not observe such a modulation of N170 to adaptors, this task-specific modulation of the adaptation effect is probably not due to such global attention shifts. While it could be argued that the effect is due to habituation, as the order of tasks was always the same, it would be at odds with other findings that report a decrease in N170 amplitude over time (Korinth et al., 2013). As we observed the opposite, namely an increase in N170 amplitude in the detail decision, we would argue that this indeed reflects a task effect.

The interaction of task × hemisphere for the adaptation effect, the difference of house ERP minus adaptor ERP, indicates a modulation of the hemispheric asymmetry of the adaptation effect triggered by demands of task. This in turn would mean that adaptation differently impacts hemispheres. Holistic adaptation is most pronounced in the right hemisphere, whereas feature-based adaptation is more pronounced in the left hemisphere, even though the effect is smaller. It is important to note, that this is true only for the adaptation effect. The N170 to test stimuli following a neutral adaptor, and which is therefore not adapted at all, did not show a hemispheric asymmetry.

Finally we would like to discuss the absence of any adaptation effects on the performance level. Obviously both tasks were easy to perform albeit more time consuming for the gender than for the detail task. The absence of adaptation effects on the performance level is most likely due to a ceiling effect in the present study. Please note that the present study seems to be the first study with the rapid adaptation paradigm that required a response to the target stimuli. It is therefore unclear whether the absence of any brain behavior relationship in the present study is a property of the paradigm or the procedural details of the present study.

Summarizing we were able to provide evidence that higher level factors can indeed influence the N170 adaptation profile. This means it is possible that low-level bottom-up processes of neural adaptation can be influenced in a top-down manner. Hence the N170 cannot necessarily be considered as reflecting a fully automatic process and can, at least to a certain extent, be modulated by higher level factors.

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Appendix.

Post hoc comparisons for N170 Latency to adaptor stimuli for different adaptors

```
Linear  Hypotheses:
                            Estimate  Std.  Error  z  value  Pr(>|z|)
 House  -   Eyes  ==  0        1.158        2.911      0.398      0.9787
 Mooney  -   Eyes  ==  0      -3.474        2.911    -1.193      0.6311
 Mouth  -   Eyes  ==  0        8.474        2.911      2.911      0.0191  *
 Mooney  -   House  ==  0     -4.632        2.911    -1.591      0.3836
 Mouth  -   House  ==  0       7.316        2.911      2.513      0.0578  .
 Mouth  -   Mooney  ==  0     11.947        2.911      4.104      <0.001  ***

---
Signif.  codes:    0  ***  0.001   **  0.01   *  0.05   .  0.1      1
(Adjusted  p  values  reported  --  single-step  method)
```

Post hoc comparisons for N170 amplitude to test stimuli

```
                            Linear  Hypotheses:

                                               Estimate Std. Error z value Pr(>|z|)
Gender. Eyes - Detail. Eyes == 0                3.2319     0.5927   5.453  < 0.001 ***
Detail. House - Detail. Eyes == 0              -4.4689     0.5927  -7.540  < 0.001 ***
Gender. House - Detail. Eyes == 0              -2.4626     0.5927  -4.155  < 0.001 ***
Detail. Mooney - Detail. Eyes == 0              0.6310     0.5927   1.065  0.96399
Gender. Mooney - Detail. Eyes == 0              2.5217     0.5927   4.255  < 0.001 ***
Detail. Mouth - Detail. Eyes == 0               1.6819     0.5927   2.838  0.08590 .
Gender. Mouth - Detail. Eyes == 0               0.9056     0.5927   1.528  0.79254
Detail. House - Gender. Eyes == 0              -7.7008     0.5927 -12.993  < 0.001 ***
Gender. House - Gender. Eyes == 0              -5.6945     0.5927  -9.608  < 0.001 ***
Detail. Mooney - Gender. Eyes == 0             -2.6009     0.5927  -4.388  < 0.001 ***
Gender. Mooney - Gender. Eyes == 0             -0.7101     0.5927  -1.198  0.93271
Detail. Mouth - Gender. Eyes == 0              -1.5499     0.5927  -2.615  0.15084
Gender. Mouth - Gender. Eyes == 0              -2.3263     0.5927  -3.925  0.00209 **
Gender. House - Detail. House == 0              2.0063     0.5927   3.385  0.01678 *
Detail. Mooney - Detail. House == 0             5.0999     0.5927   8.605  < 0.001 ***
Gender. Mooney - Detail. House == 0             6.9906     0.5927  11.795  < 0.001 ***
Detail. Mouth - Detail. House == 0              6.1508     0.5927  10.378  < 0.001 ***
Gender. Mouth - Detail. House == 0              5.3745     0.5927   9.068  < 0.001 ***
Detail. Mooney - Gender. House == 0             3.0936     0.5927   5.220  < 0.001 ***
Gender. Mooney - Gender. House == 0             4.9844     0.5927   8.410  < 0.001 ***
Detail. Mouth - Gender. House == 0              4.1446     0.5927   6.993  < 0.001 ***
Gender. Mouth - Gender. House == 0              3.3682     0.5927   5.683  < 0.001 ***
Gender. Mooney - Detail. Mooney == 0            1.8907     0.5927   3.190  0.03079 *
Detail. Mouth - Detail. Mooney == 0             1.0509     0.5927   1.773  0.63841
Gender. Mouth - Detail. Mooney == 0             0.2746     0.5927   0.463  0.99980
Detail. Mouth - Gender. Mooney == 0            -0.8398     0.5927  -1.417  0.84973
Gender. Mouth - Gender. Mooney == 0            -1.6162     0.5927  -2.727  0.11435
Gender. Mouth - Detail. Mouth == 0             -0.7764     0.5927  -1.310  0.89541
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1
(Adjusted p values reported -- single-step method)
```

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